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Characterization of western corn rootworm (Coleoptera: Chrysomelidae) population dynamics in relation to landscape attributes

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Abstract

1 The western corn rootworm (WCR), *Diabrotica virgifera virgifera* Leconte (Coleoptera: Chrysomelidae), creates economic and environmental concerns in the Corn Belt region of the U.S.A. To supplement the population control tactics of the Areawide Pest Management Program in Brookings, South Dakota, Geographical Information Systems (GIS) were used to examine the spatial relationships from 1997 to 2001 between WCR population dynamics, habitat structure, soil texture and elevation.

2 Using the inverse distance weighted interpolation technique, WCR population density maps were created from georeferenced emergence and post-emergence traps placed in maize fields. For each year, these maps were overlaid with vegetation, soil and elevation maps to search for quantitative relationships.

3 Through visual interpretation and correlation analysis, shifts in landscape structure, such as size, number and arrangement of patches, were shown to associate with WCR population abundance and distribution in varying degrees. Contingency analysis showed that WCR population abundance is associated with soil texture and elevation.

4 An understanding of the interactions between WCR population dynamics and landscape variables provides information to pest managers, and this can be used to identify patterns in the landscape that promote high insect population density patches to improve pest management strategies.

Keywords Geographic Information Systems (GIS), landscape metrics, population dynamics, spatial analysis, western corn rootworm (WCR).

Introduction

The western corn rootworm (WCR), *Diabrotica virgifera virgifera* Leconte (Coleoptera: Chrysomelidae), is a serious insect pest of maize *Zea mays* L., in the US Corn Belt (Kantack *et al*., 1970; Metcalf, 1986). Local abundance and spatial distribution of adult WCR is influenced by cropping practices (Hill and Mayo, 1980). The western corn rootworm tends to be found in maize fields throughout its life and may move locally from more mature to less mature maize. This considerable interfield movement occurs in areas where season length and cultural practices result in the presence of maize at varying maturities. Traditional control methods include the use of insecticides and crop rotation. However, insecticides are often used unnecessarily, and this indiscriminate use of soil insecticides has promoted environmental (i.e. runoff, groundwater alterations, etc.), safety (i.e. handling) and economic concerns (Gray *et al*., 1993). In addition, some female WCR began laying eggs outside of maize fields, usually soybean, *Glycine max* (L.) Merrill, fields (Onstad *et al*., 1999; Levine *et al*., 2002). Therefore, failure of crop rotation as a consistent and economical means of managing WCR populations and the development of insecticide resistance has prompted the need for new management tactics (Siegfried *et al*., 1998; Tollefson, 1998; Wilde *et al*., 1998; Levine *et al*., 2002).

To help alleviate these concerns, the United States Department of Agriculture (USDA), Agricultural Research

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Service (ARS) implemented a corn rootworm areawide pest management initiative in 1996 (Chandler and Faust, 1998; Chandler *et al*., 2000). This initiative was established in five geographical locations, four in the US Corn Belt and one in Texas (Chandler and Faust, 1998; Tollefson, 1998; Wilde *et al*., 1998). The areawide approach relies on management of adult rootworm populations over a wide geographical area using action thresholds. Action thresholds are used to determine appropriate timing for aerial applications of toxic bait formulations that substantially diminish the amount of applied pesticide (Chandler and Faust, 1998). To supplement the areawide approach and to document interactions of edaphic and landscape factors with the WCR, the present study focused on analysing spatial relationships between WCR population dynamics and habitat structure, soil texture and elevation. Understanding these relationships is important for directing future pest management decisions at a landscape scale (Landis, 1994). Accordingly, Geographical Information Systems (GIS) were used that allow the creation of map layers for visual interpretation and geostatistical analysis of spatial interactions at larger scales (Roberts *et al*., 1993; Stow, 1993). Our objectives were: (i) to document shifts in landscape structural characteristics from 1997 to 2001 in relation to WCR population dynamics and (ii) to detect the relationships of soil texture and elevation with WCR population dynamics.

Methods

Description of study area

The South Dakota corn rootworm areawide management site was located in the western portion of the US Corn Belt (Universal Transverse Mercator coordinates in metres, NW corner 681127E, 4911981N, NE corner 687618E, 4912125N, SW corner 681317E, 4905524W, and SE corner 687768E, 4905671N) in Brookings County, South Dakota. The study site was within the tall-grass prairie region of the northern Great Plains (Kaul, 1986), encompassed 41.4 km^2, and was dominated by a mosaic of maize-soybean cropping systems. The site contained approximately 60 maize fields and 60 soybean fields, depending on the year. We used this management area to characterize the spatial dynamics of WCR over a 5-year period (1997–2001).

Trap collection

Western corn rootworm populations were monitored weekly with emergence traps and Pherocon AM® (Trécé Inc., Salinus, CA) yellow sticky traps (post-emergence) (Tollefson, 1986). The traps were placed in the maize fields approximately 60 m apart along two transects during late June to early July of each year, depending on weather conditions. Post-emergence traps were placed in 55–62 maize fields, whereas emergence traps were placed in 11–16 maize fields, depending on the year. The number of emergence and post-emergence traps used in each field varied with field size. Twelve traps were placed in 'A' fields ($\geq$ 47 ha), nine traps in 'B' fields (25–46 ha), six traps in 'C' fields (10–24 ha) and three traps in 'D' fields ($\leq$ 9 ha). The emergence traps (1.0×0.6 m) were placed length-wise directly over five cut plants in the maize row to capture beetles as they emerged from the soil. Post-emergence traps (0.2×0.3 m) were clamped onto wood lathes placed between maize rows within each field. We placed these post-emergence traps at ear height of the maize plant, or approximately 1 m above the soil surface. As beetles flew through the field, they were captured on the adhesive surface of the trap. Post-emergence traps were collected weekly for approximately 10 weeks. Emergence traps were collected weekly until only a few beetles were being captured (approximately 7 weeks). The weekly totals were combined for each year from 1997 to 2001.

Georeferencing and crop association

The trap and field locations were georeferenced and crop or vegetation types were documented yearly. Vector map layers were created for the study site using a differential Global Positioning System. Vector maps portray spatial features as points (traps), lines (roads) and polygons (crop fields) (Bonham-Carter, 1994; Johnston, 1998). Attribute tables associated with vector maps contain information about the spatial features (e.g. trap type). For each year, we imported the following attributes: field locations, field sizes, crop types, trap locations, trap types and the number of WCR captured. Crop types were classified as continuous maize, first-year maize, mixed maize and soybeans. The soybean classification was deemed important because of the prominence of maize-soybean rotations in the management site. Continuous maize fields were fields that were planted to maize for two or more consecutive years. First-year maize fields were fields planted to a crop other than maize the previous year (usually soybeans). Mixed maize fields were those that contained a portion of both continuous maize and first-year maize. Other maize fields included sweet maize or maize test plots. Mixed and other maize fields made up only a small portion of the maize planted in the management site. Thus, they were not used in patch-level analyses but only in all maize class-level analyses (see below). Trap types were classified into emergence and post-emergence traps.

Interpolation techniques

Areas of abundance and distribution of WCR based on emergence and post-emergence activity in maize were characterized as raster map layers (26.4 m cell size) using Inverse Distance Weighted (IDW) interpolation techniques. By contrast to vector maps, raster maps portray spatial features as a matrix of equal-area grid cells containing unique values (Bonham-Carter, 1994; Johnston, 1998). Interpolation methods calculate predicted variable values for unsampled areas using georeferenced point sample locations (Kopp *et al*., 2002). The IDW method of interpolation estimates the values of sample data points in the vicinity of each cell of the surface map. The closer the point is to the cell centre being estimated, the more influence it has in the averaging process. With IDW, the exponent or power value controls the significance of known georeferenced points upon the interpolated values, based upon the distance from the output point (Kopp *et al*., 2002). The most commonly used exponent value of two was used, resulting in a smooth raster surface. A variable search radius, with 12 input points was used to allow for variable search neighbourhoods, depending on the density of measured points near the interpolated cell (Kopp *et al*., 2002). There were several reasons that the IDW method was used to estimate beetle abundance. The IDW algorithm allows for rapid calculation, is good for analysing short range variability between scattered data points, is appropriate for aggregated data, and generates quick contour plots for relatively smooth data values (Krajewski and Gibbs, 2001).

We used the WCR interpolated maps along with the vegetation maps to visually analyse their spatial relationships. However, to describe general relationships in quantitative terms, or to map the distribution of varying degrees of correspondence between maps, would be impossible from visual inspection alone. Therefore, interpolated maps, classified maps of vegetation and the landscape metrics were compared to determine relationships between habitat structure and WCR population dynamics.

Landscape metrics

Landscape metrics were calculated using FRAGSTATS software (University of Massachusetts, Amherst, MA) to examine relationships between changes in landscape structure and WCR population dynamics over the management site comprising 4144 ha. Vegetation (vector) maps were converted into raster maps from which FRAGSTATS calculated class-level and patch-level landscape metrics. Patch-level metrics focus on individual fields of a particular vegetation type (e.g. all maize or continuous maize), whereas class-level metrics focus on groups of fields of a particular vegetation type (e.g. all maize or continuous maize) (McGarigal *et al*., 2002). The patch-level metrics included patch area in hectares, proximity index of each patch, and the nearest neighbour distance in metres of each patch. The class-level metrics included total class area in hectares, percent of the landscape occupied by each class, number of patches in each class, mean patch size in hectares of each class, mean proximity index of each class and mean nearest neighbour distance in metres of each class.

At the class-level, area and percent of landscape occupied by patches are indicators of landscape composition; specifically, how much of the landscape is comprised by a particular patch type (McGarigal *et al*., 2002). In addition, the number and arrangement of patches of a particular habitat type may influence ecological processes within a landscape. For example, the number of patches may determine the number of subpopulations for species exclusively associated with that habitat type, whereas the arrangement of patches may affect dispersal rates among the preferred habitats.

We used nearest neighbour and proximity analyses to determine patch arrangement (McGarigal *et al*., 2002). Nearest neighbour analysis is calculated by measuring the shortest straight-line distance between the focal patch and its nearest neighbour of the same habitat type. However, at the class-level, mean nearest neighbour does not adequately describe the spatial distribution of patches. This difficulty can be overcome to a certain extent by reporting the standard deviation around the mean, as a measure of patch dispersion. A large standard deviation relative to the mean implies an uneven or irregular distribution, whereas a small standard deviation about the mean indicates a uniform or regular distribution (McGarigal *et al*., 2002). The measure only applies to distances between patches in a cluster, ignoring the potentially vast distance between the edge of the cluster and the edge of the map (Hargis *et al*., 1998).

The proximity index was developed to overcome the limitations of nearest neighbour distance. It considers the size and proximity of all patches whose edges are within a specified search radius of the focal patch (McGarigal *et al*., 2002). The proximity index determines the spatial arrangement of a habitat patch in relation to its neighbours of the same class; specifically, the index differentiates sparse distributions of small habitat patches from a complex cluster of larger patches. The proximity index can be applied where patches of interest occur in low densities and under different degrees of isolation, such as the study of spatial patterns of metapopulations. Landscapes with aggregated large patches have higher proximity values than landscapes with dispersed smaller patches (Hargis *et al*., 1998).

To ascertain relationships between landscape metrics and WCR population dynamics, we performed correlation analysis between patch-level metrics with mean number of WCR post-emergence captured and class-level metrics with the total and mean number of WCR post-emergence captured. These analyses were conducted on continuous maize, first-year maize and all maize classes. For patch-level metrics, the all maize class included continuous and first-year maize fields whereas, for class-level metrics, the all maize class included continuous, first-year maize and other maize fields that contained post-emergence traps. All data were transformed to $\log_{10}(n+1)$ to normalize distributions and equalize variances (Zar, 1984). Significance of each correlation coefficient was determined from a Fisher's r to z transformation (SAS Institute, 1998).

Emergence and post-emergence correlation

Western corn rootworm emergence probably correlates with optimal conditions for oviposition and larval survival and should associate with edaphic factors such as soil texture and topography (Tollefson and Calvin, 1994). However, because the number of emergence traps in the management site was much fewer than the number of post-emergence traps, and post-emergence traps encompassed all elevation classes and soil types, we believe the post-emergence interpolated maps would provide a more accurate estimate of the WCR spatial associations with soil texture and elevation. To employ post-emergence interpolated maps to analyse relationships between WCR dynamics, soil texture and elevation, we first aimed to determine the relationship between WCR emergence and post-emergence. Two statistical methods were used to investigate the significance of this relationship. The first correlation was computed within ArcInfo software (ESRI, Redlands, CA) by overlaying the interpolated emergence and post-emergence map layers (Chou, 1997). The second correlation was computed using the mean number of WCR captured in emergence and post-emergence traps in each patch, which allowed a direct comparison between fields that contained only emergence and post emergence traps. These data were transformed to $\log_{10}$ (n + 1) (Zar, 1984). Significance of each correlation coefficient from interpolated map analysis was determined from a table of critical values of the correlation coefficient (Zar, 1984). Significance of each correlation coefficient from the second analysis (tabular data) was determined from a Fisher's r to z transformation (SAS Institute, 1998).

Contingency analysis

The soils data covering Brookings County were acquired as a vector map from the United States Geological Survey (USGS) online Soil Survey Geographic (SSURGO) database (www.ftw.nrcs.usda.gov/ssur_data.html). The soil texture map (scale 1 : 24 000) was converted into a raster map with 26.4-m cell size to match the cell size of the WCR interpolated maps. The soil map was then classified into five classes corresponding to soil textures found within the management site. Soil texture classes ranged from least porous to most porous based on the composition of particle size associated with the general soil texture triangle (Buckman and Brady, 1969). The texture classes included silty clay, silty clay loam, silt loam, loam and sandy loam.

The USGS Digital Elevation Model (DEM) covering Brookings County was acquired as a raster map from an online database (www.gisdatadepot.com). This comprises a georeferenced digital map and attribute data in a quadrangle format with a scale of 1 : 24 000 (30-m cell size). The DEM was reclassified with 26.4-m cell size to match the cell size of the WCR interpolated maps. The elevation map was then reclassified into a new raster map with five equal-interval elevation classes. The elevation classes included Class 1 (494–499 m), Class 2 (500–504 m), Class 3 (505–509 m), Class 4 (510–514 m) and Class 5 (515–519 m).

Interpolated raster maps were classified by year into five classes (showing the number of WCR captured/trap). The natural breaks classification scheme was used to identify natural groupings of data based on breakpoints inherent in the data (Abler *et al.*, 1971; Monmonier, 1977; Hatakeyama *et al.*, 2000). For each year, we classified WCR populations as low, low to medium, medium, medium to high and high. Over the 5 years, low values ranged from 0–18 to 0–42, low to medium values ranged from 19–44 to 43–162, medium values ranged from 45–71 to 163–355, medium to high values ranged from 72–153 to 356–1100 and high values ranged from 130–278 to 1103–1137. Each of the map layers, soils, elevation and population was imported into Idrisi GIS software (Clark Laboratories-Clark University, Worcester, MA) and masked to display only the soil texture classes, elevation classes and interpolated values found in maize fields. This was necessary because we were concerned only with the statistical relationships in WCR preferable habitat and environmental variables.

Within Idrisi, contingency analysis compares the categories of one image (i.e. raster map layer) with those of a second image. Tabulation was kept of the frequency of cells in each possible combination of both variables (i.e. population and soil texture or population and elevation) and measures of association were computed between the images (Eastman, 2001). These measures included chi-square statistics and Cramer's V coefficients that indicate the degree of association between the variables (Ott *et al.*, 1983; Siegel and Castellan, 1988; Bonham-Carter, 1994). Significance of each chi-square statistic was determined from a table of critical values of the chi-square distribution (Zar, 1984).

Results

Landscape metrics

The total class area, percent of landscape and number of patches occupied by continuous maize decreased from 1997 to 2001 as did the total number of WCR captured, but not mean number of WCR captured (Table 1). In addition, only the total number of WCR captured correlated significantly with class area, percent of landscape and number of patches (Table 2). With the decrease in continuous maize over the 5 years, there was an associated increase in crop rotation resulting in an overall increase in class area, percent occupied and number of patches of first-year maize and soybeans (Table 1). There were no significant correlations between class area, percent of landscape and number of patches with total and mean number of WCR captured in first-year maize fields (Table 2). The class area, percent of landscape and number of patches occupied by all maize peaked in 1998 and were least in 2001 (Table 1). With the exception of total WCR captured and percent of landscape, there were significant correlations between class area, percent of landscape and number of patches with total and mean number of WCR captured in all maize (Table 2).

The mean patch size and mean proximity values for continuous maize peaked in 1998, then steadily declined through 2001. However, the mean nearest neighbour values peaked in 2001 and varied in the four preceding years (Table 1). We found a significant correlation only between mean proximity and total number of WCR captured in continuous maize (Table 2). The mean patch size of first-year maize remained relatively constant over the 5-year period, with a mean maximum difference of 5.3 ha between 1998 and 2001. The mean proximity value for first-year maize was highest in 2000 and least in 1997, whereas the mean nearest neighbour value was highest in 1997 and least in 2001 (Table 1). There were no significant correlations between mean patch size, mean proximity and mean nearest neighbour with total and mean number of WCR captured in first-year maize (Table 2). Similar to first-year maize, the mean patch size for all maize also remained relatively constant over the 5-year period, with a mean maximum differ-

Table 1 Class-level landscape metrics computed for all vegetation types

Type	CA	%	NP	Area ± SD	Prox ± SD	NN ± SD	WT	WCR ± SD
1997								
C	316	8	12	26.3 ± 18.6	28.0 ± 35.9	555.2 ± 510.4	5592	6.9 ± 12.6
F	938	23	41	22.9 ± 18.1	70.8 ± 75.2	132.1 ± 149.7	3222	1.3 ± 3.1
A	1352	33	60	22.3 ± 18.4	151.6 ± 139.6	102.9 ± 113.4	9135	3.4 ± 8.6
S	1173	28	55	21.3 ± 16.8	121.3 ± 109.6	101.9 ± 86.9	—	—
1998								
C	282	7	10	28.2 ± 21.9	130.3 ± 129.5	455.1 ± 670.2	8800	14.6 ± 28.7
F	962	23	49	19.6 ± 15.6	87.2 ± 81.4	115.0 ± 127.2	3935	1.7 ± 3.7
A	1370	33	73	18.1 ± 16.4	142.0 ± 130.6	78.2 ± 57.2	13 747	4.5 ± 14.4
S	1226	30	56	21.9 ± 17.1	117.5 ± 94.7	98.8 ± 113.9	—	—
1999								
C	243	6	11	22.1 ± 20.4	53.0 ± 82.0	585.5 ± 793.8	6842	12.2 ± 39.6
F	989	24	43	23.0 ± 14.4	93.0 ± 84.9	111.7 ± 121.1	2337	1.1 ± 2.4
A	1278	31	60	21.0 ± 16.1	121.4 ± 116.9	98.5 ± 114.5	9212	3.2 ± 18.3
S	1211	29	57	21.3 ± 16.0	113.3 ± 92.9	89.0 ± 80.3	—	—
2000								
C	158	4	8	19.8 ± 19.0	8.4 ± 11.8	439.4 ± 336.9	4787	11.2 ± 21.4
F	1088	26	48	22.7 ± 16.0	101.9 ± 87.0	93.4 ± 82.3	7194	2.6 ± 5.1
A	1303	31	59	21.8 ± 16.1	127.4 ± 92.1	87.4 ± 78.5	12 624	3.9 ± 9.8
S	1291	31	53	24.3 ± 18.4	149.5 ± 111.3	80.7 ± 76.1	—	—
2001								
C	78	2	4	19.6 ± 20.2	0.0 ± 0.0	979.6 ± 2.8	2134	11.9 ± 17.1
F	1048	25	42	24.9 ± 15.8	98.2 ± 83.9	100.1 ± 108.0	2112	0.9 ± 3.8
A	1133	27	48	23.5 ± 16.5	97.8 ± 85.2	119.6 ± 138.8	4246	1.7 ± 6.5
S	1225	30	60	20.4 ± 16.3	113.6 ± 83.5	72.9 ± 57.7	—	—

Classes include continuous maize (C), first-year maize (F), all maize (A) and soybean (S). Metrics include total class area (CA), percent of the landscape occupied (%), number of patches (NP), mean patch size or area (Area ± SD), mean proximity index (Prox ± SD), mean nearest neighbour distance (NN ± SD), total number of WCR post-emergence (WT) and number of WCR post-emergence captured/week/trap (WCR ± SD).

ence of 5.4 ha between 1998 and 2001 (Table 1). The mean proximity value for all maize was highest in 1997 and least in 2001, whereas the mean nearest neighbour value was highest in 2001 and least in 1998 (Table 1). We found significant correlations only between mean nearest neighbour and total and mean number of WCR captured in all maize (Table 2).

By visually inspecting and comparing the interpolated WCR population raster maps to the classified vegetation maps over the 5-year period, it is evident that the spatial distribution of WCR post-emergence in the management site was concentrated mainly in continuous maize patches and adjacent maize patches (Figs 1–5). Note that, as the distribution of continuous maize patches shifted in the management site over the 5-year period, the corresponding distribution of WCR also shifted. This is partially corroborated by the significant class-level correlations for continuous maize between mean proximity values and total number of WCR captured, and class-level correlations for all maize between mean nearest neighbour and total and mean number of WCR captured (Table 2). Further evidence is indicated by the significant patch-level correlations between post-emergence captures in first-year maize and all maize with patch area, patch proximity, and patch nearest neighbour (Table 3).

There were no significant correlations between mean number of WCR post-emergence in continuous maize and all patch-level landscape metrics (Table 3). However, in first-year maize, significant correlations were found between patch area, patch proximity and patch nearest neighbour with mean number of WCR captured in the post-emergence traps (Table 3). A negative correlation was found between mean number of WCR post-emergence in first-year maize and nearest neighbour distance. There were significant correlations between mean number of WCR post-emergence in all maize and patch area and proximity, but not nearest neighbour distance (Table 3).

Contingency analysis

We found significant correlations between WCR emergence and post-emergence interpolated maps for all five years (Table 4). We also found significant correlations between mean numbers of WCR captured from emergence and post-emergence traps for each of the 5 years (Table 4). The correlation coefficient also was significant over all 5 years ($r = 0.84$, d.f. = 60, $P = < 0.001$). Therefore, we used post-emergence interpolated maps to determine relationships between soil texture and elevation.

Loam was the most common soil texture class (47.7%) in the management site, followed by silty clay loam (31.4%), silt loam (17.7%), sandy loam (2.9%) and silty clay (0.3%) Western corn rootworm populations occurred most frequently on loam and silty clay loam soil textures (Table 5). Contingency analysis revealed highly significant associations

Table 2 Correlation coefficients (r) between class-level landscape metrics with total number of western corn rootworm (WCR) and mean number of WCR post-emergence captured/week/trap by vegetation type

		Total WCR			Mean WCR		
Type	Metric	*N*	*r*	*P*	*N*	*r*	*P*
C	CA	5	0.92	<0.05	5	−0.27	0.70
F		5	0.36	0.60	5	0.38	0.58
A		5	0.91	<0.05	5	0.94	<0.05
C	%	5	0.90	<0.05	5	−0.29	0.67
F		5	0.35	0.60	5	0.36	0.60
A		5	0.86	0.06	5	0.91	<0.05
C	NP	5	0.90	<0.05	5	−0.31	0.66
F		5	0.73	0.19	5	0.79	0.13
A		5	0.89	<0.05	5	0.92	<0.05
C	Area	5	0.73	0.18	5	−0.12	0.86
F		5	−0.42	0.53	5	−0.46	0.48
A		5	−0.74	0.18	5	−0.76	0.16
C	Prox	5	0.99	<0.01	5	0.11	0.88
F		5	0.17	0.81	5	0.22	0.75
A		5	0.61	0.32	5	0.68	0.25
C	NN	5	−0.83	0.09	5	−0.04	0.96
F		5	−0.33	0.62	5	−0.37	0.58
A		5	−0.94	<0.05	5	−0.94	<0.05

Classes include continuous maize (C), first-year maize (F) and all maize (A). Metrics include total class area (CA), percent of the landscape occupied (%), number of patches (NP), mean patch size or area (Area), proximity index (Prox) and nearest neighbour distance (NN). Also included are number of years (N) and probability values (*P*) for *r*.

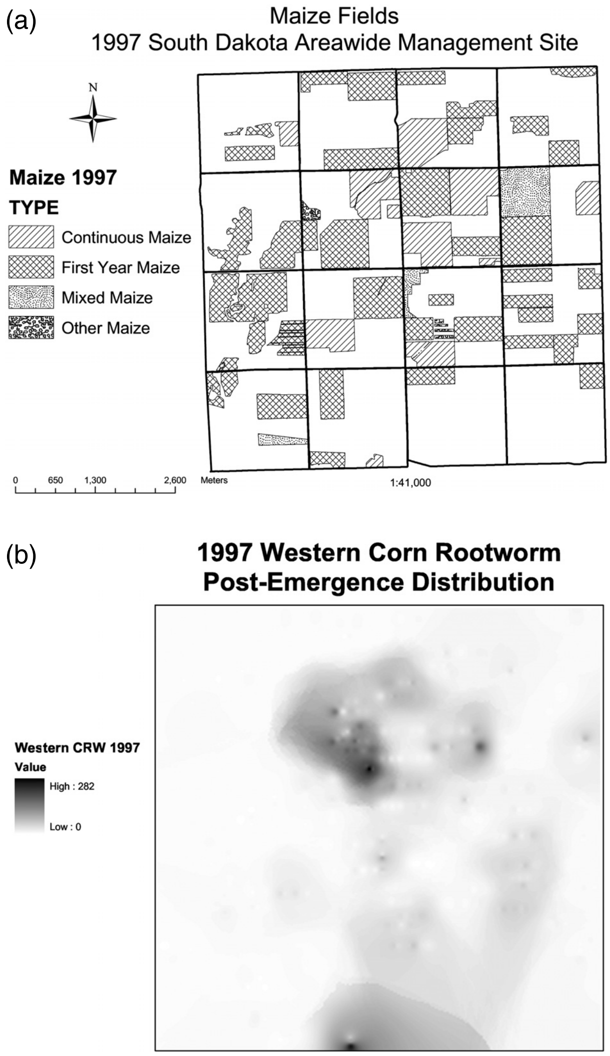

Figure 1 (A) Vector map illustrating roads and maize fields found in the South Dakota areawide management site in 1997. (B) Raster map illustrating interpolated values of western corn rootworm (WCR) post-emergence in the South Dakota areawide management site in 1997.

between soil texture and WCR abundance for each year, as indicated by chi-squared (Table 6). The strength of the association was greatest in both 1997 and 2001 and least in 1999 as indicated by Cramer's V coefficients (Table 6).

Class 2 (34.6%) was the most common elevation in the management site followed by Class 1 (24.1%), Class 3 (22.4%), Class 4 (17.7%) and Class 5 (1.2%). Western corn rootworm populations occurred most frequently on elevation classes 2 and 3 (Table 7). Contingency analysis revealed highly significant associations between elevation class and WCR abundance for each year, as indicated by chi-squared Table 8). The strength of the association was greatest in both 1998 and 2000 and least in 2001 as indicated by Cramer's V coefficients (Table 8).

Discussion

Landscape metrics

Basic structural characteristics of the landscape can affect species abundance and distribution (Turner, 1989; Wiens, 1997; McGarigal *et al*., 2002). The abundance and distribution of many species may be strongly correlated with the total area and number of patches of preferred habitat within the context of the landscape (Forman and Godron, 1986; Forman, 1995). In our study, WCR total abundance, but not mean abundance, correlated with class area, percent of landscape and number of patches of continuous maize. Furthermore, neither total nor mean WCR abundance correlated with class area, percent of landscape, and number of patches of first-year maize. This suggests that WCR are dispersing from continuous maize fields, the primary source of WCR production, into first-year maize fields, which are acting as sink habitats (Chiang, 1973; Pulliam and Danielson, 1991; Forman, 1995; Chandler *et al*., 2000; Levine *et al*., 2002). This is partially corroborated by correlations between total and mean WCR abundance with class area, percent of landscape, and number of patches of all maize, and the lack of correlations between mean WCR abundance with these landscape metrics in continuous maize.

Large aggregated patches may support higher densities than smaller dispersed patches (Harrison and Taylor, 1997;

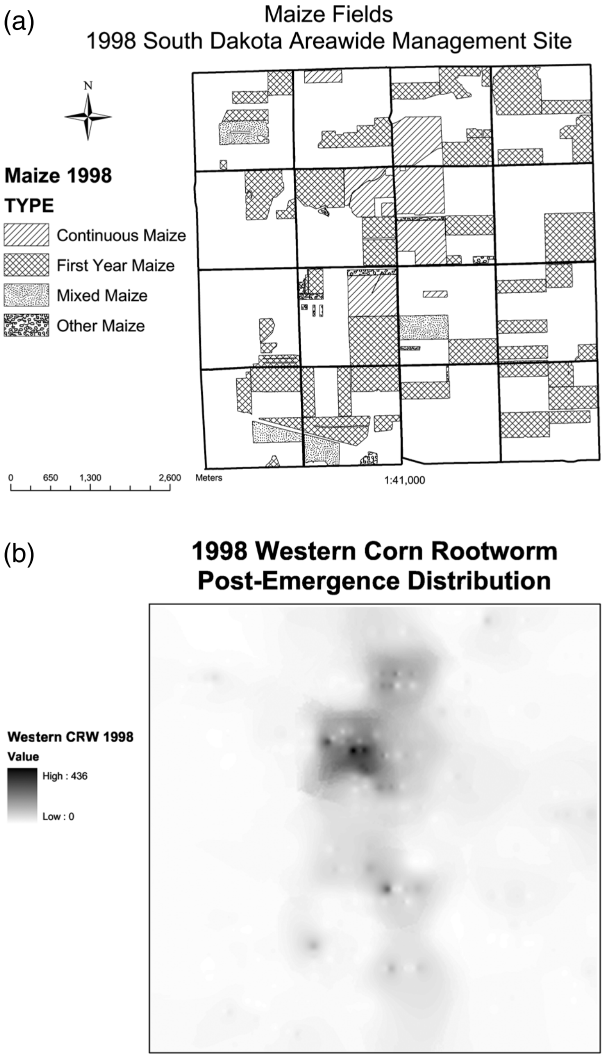

Figure 2 (A) Vector map illustrating roads and maize fields found in the South Dakota areawide management site in 1998. (B) Raster map illustrating interpolated values of western corn rootworm (WCR) post-emergence in the South Dakota areawide management site in 1998.

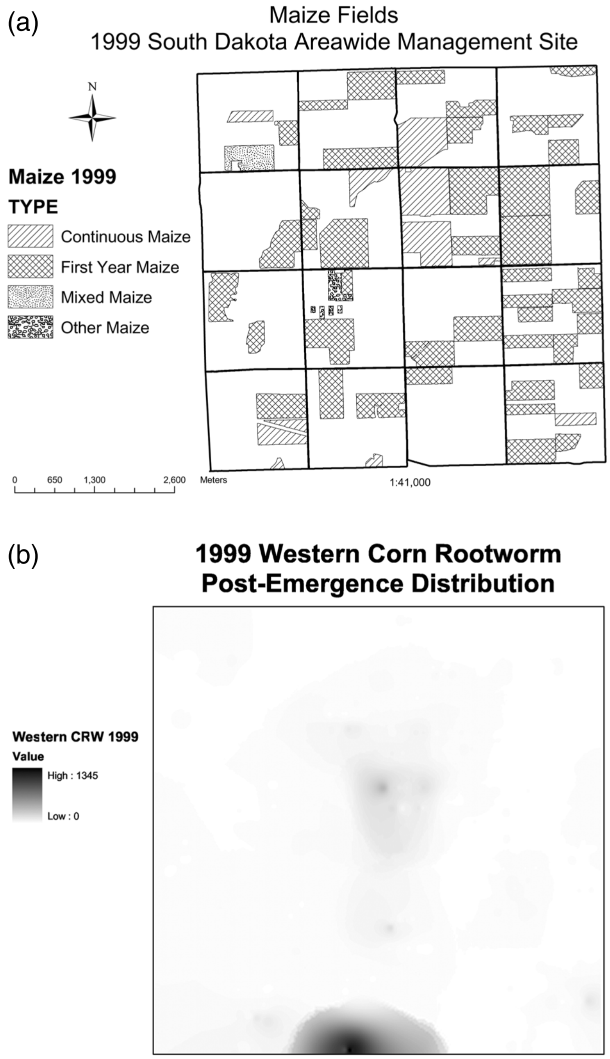

Figure 3 (A) Vector map illustrating roads and maize fields found in the South Dakota areawide management site in 1999. (B) Raster map illustrating interpolated values of western corn rootworm (WCR) post-emergence in the South Dakota areawide management site in 1999.

Wiens, 1997). For example, Thomas and Hanski (1997) found that large habitat patches in close proximity had a higher frequency of the skipper butterfly *Hesperia comma* than smaller, more isolated patches. Similarly, Smith and Gilpin (1997) found that, in all cases for the American pika *Ochtona princeps*, the average size of occupied patches was greater than the average size of vacant patches. The maize fields in the management site varied in size and arrangement over the 5-year period. Through visual map interpretation, nearest neighbour analyses and proximity analyses, we showed that continuous, first-year and all maize vegetation types shifted in their size and dispersion patterns in the management site over the 5-year period. In response, WCR abundance shifted to the availability of maize patches. Supporting this notion is the positive class-level correlation between WCR total abundance and proximity of continuous maize, and the inverse relationships between WCR total and mean abundance with mean nearest neighbour distance in all maize. Furthermore, the lack of patch-level and class-level correlations between mean WCR abundance with patch area, proximity and nearest neighbour of continuous maize suggests these fields reach their carrying capacities quickly, and WCR disperse in search of habitat patches away from their natal patch. Even though WCR are capable of dispersing long distances (Coats *et al.*, 1986), large, first-year maize patches in close proximity to continuous maize attracted more WCR than smaller, more distant patches. This evidence is supported by the patch-level relationships of mean WCR abundance with patch area and proximity in first-year and all maize, and the inverse relationship with nearest neighbour in first-year maize.

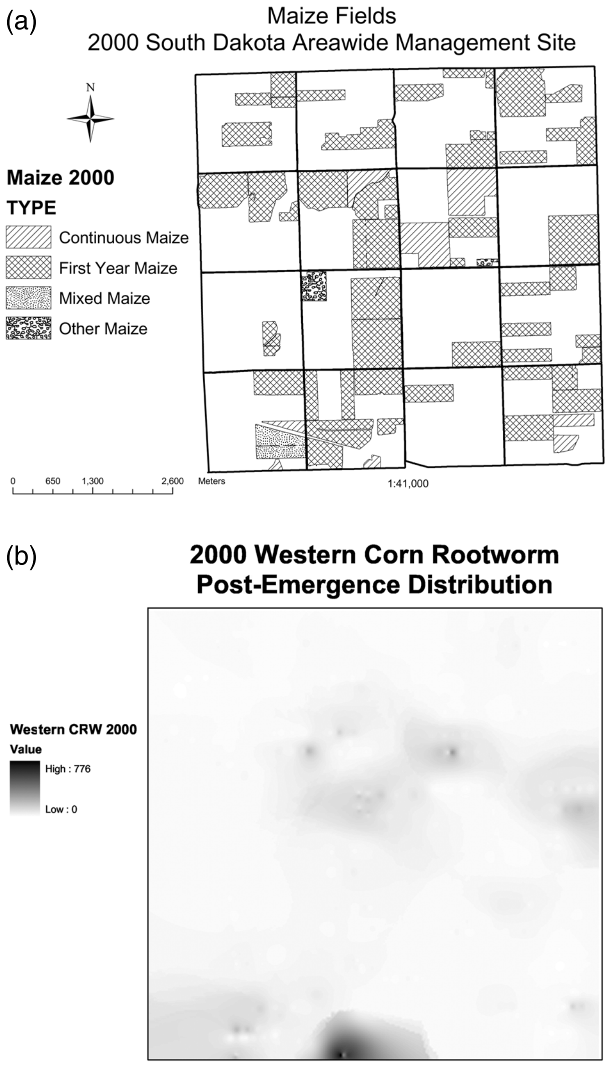

Figure 4 (A) Vector map illustrating roads and maize fields found in the South Dakota areawide management site in 2000. (B) Raster map illustrating interpolated values of western corn rootworm (WCR) post-emergence in the South Dakota areawide management site in 2000.

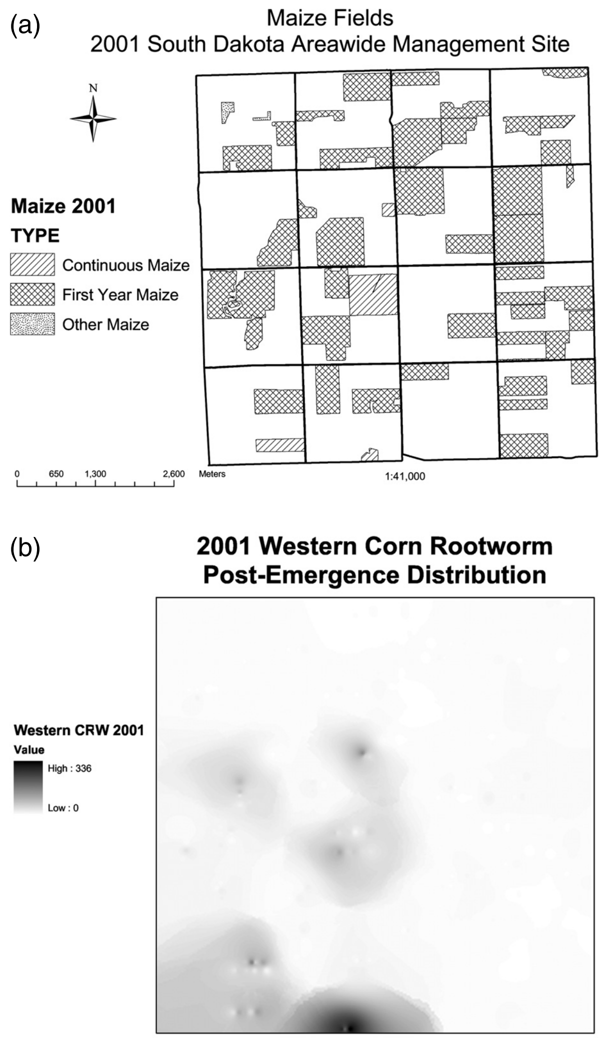

Figure 5 (A) Vector map illustrating roads and maize fields found in the South Dakota areawide management site in 2001. (B) Raster map illustrating interpolated values of western corn rootworm (WCR) post-emergence in the South Dakota areawide management site in 2001.

Contingency analysis

In addition to structural characteristics of landscape configuration, edaphic factors can influence the distribution of populations. For example, the microhabitat of a preferred oviposition site for female corn rootworms is influenced by soil properties such as type, texture, moisture content and compaction (Kirk *et al.*, 1968; Ruesink, 1986). The distribution and abundance of WCR in the management site was highly associated with both soil texture and elevation. We found WCR in greater proportions than expected on loam and silty clay loam soils, and on elevations between 500 m and 509 m (Classes 2 and 3). The variability in soil texture at our site was comparable to a laboratory study that showed survival rate of WCR and southern corn rootworm *Diabrotica undecimpunctata howardi* Barber larvae depended on

Table 3 Correlation coefficients (r) between patch-level landscape metrics with mean number of western corn rootworm post-emergence captured/patch/trap by vegetation type

Type	Metric	N	r	P
C	Area	42	0.10	0.54
F		222	0.25	<0.001
A		264	0.16	<0.01
C	Prox	42	0.18	0.25
F		222	0.19	<0.01
A		264	0.20	<0.01
C	NN	42	−0.13	0.41
F		222	−0.14	<0.05
A		264	−0.08	0.23

Classes include continuous maize (C), first-year maize (F) and all maize (A). Metrics include patch area (Area), proximity index (Prox) and nearest neighbour distance (NN). Also included are number of fields from 1997 to 2001 (N) and probability values (P) for r.

Table 4 Correlation coefficients between western corn rootworm (WCR) emergence and post-emergence interpolated map layers (Interpolated) and between WCR mean emergence and mean post-emergence (Tabular) for 1997–2001

	Interpolated			Tabular		
Year	*N*	*r*	*P*	*N*	*r*	*P*
1997	62 750	0.71	<0.001	10	0.85	<0.002
1998	62 750	0.88	<0.001	11	0.86	<0.001
1999	62 750	0.78	<0.001	15	0.84	<0.001
2000	62 750	0.74	<0.001	11	0.79	<0.005
2001	62 750	0.86	<0.001	15	0.98	<0.001

Variables include year, number of observations (*N*), correlation coefficients (*r*) and probability values (*P*). Degrees of freedom = $N - 2$.

the clay percentage of the soil and porosity, which are both functions of soil texture (Turpin and Peters, 1971).

Historically, managing pest insect populations in agricultural ecosystems has occurred at the farm scale rather than at the landscape scale (Brewster *et al*., 1999; Landis *et al*., 2000). The corn rootworm areawide management program was established to suppress adult corn rootworms over a broad area using action thresholds to trigger aerial applications of bait attraction insecticides. Therefore, the areawide approach to managing corn rootworm populations encompasses particular features of the agricultural landscape, such as size and arrangement of patches, which can be used to examine

Table 5 Cell frequencies for contingency analysis between soil texture and interpolated western corn rootworm (WCR) abundance maps

	Soil texture class				
WCR class	SiC	SiCL	SiL	L	SaL
1997					
Low	0	4072	1898	6211	521
Low to medium	9	2118	929	512	0
Medium	47	717	286	787	0
Medium to high	66	31	78	489	15
High	1	39	73	322	19
1998					
Low	28	3587	1966	7263	429
Low to medium	5	917	1136	1639	3
Medium	42	551	268	659	1
Medium to high	65	46	183	468	29
High	0	14	22	327	6
1999					
Low	111	6012	2606	6984	780
Low to medium	14	846	150	582	0
Medium	0	7	0	64	0
Medium to high	0	0	30	1	0
High	0	0	27	0	0
2000					
Low	29	2711	2416	7025	269
Low to medium	66	1470	189	1924	57
Medium	3	610	31	1331	4
Medium to high	0	298	0	186	0
High	0	1	57	0	0
2001					
Low	52	5340	1744	6142	730
Low to medium	0	1	97	798	0
Medium	0	0	503	365	0
Medium to high	0	5	121	253	0
High	0	0	57	1	0

Variables include classes of WCR abundance (WCR class) and soil texture classes, including silty clay (SiC), silty clay loam (SiCL), silt loam (SiL), loam (L) and sandy loam (SaL).

Table 6 Contingency statistics for soil texture and western corn rootworm abundance

Year	Chi squared	d.f.	Cramer's V	P
1997	3383	16	0.21	<0.001
1998	1832	16	0.15	<0.001
1999	608	16	0.09	<0.001
2000	1900	16	0.16	<0.001
2001	2803	16	0.21	<0.001

Variables include year, chi squared, degrees of freedom (d.f), Cramer's V coefficient, and probability value (*P*).

Table 7 Cell frequencies for contingency analysis between elevation and interpolated western corn rootworm (WCR) abundance maps

	Elevation class				
WCR class	1	2	3	4	5
1999					
Low	2266	3683	3613	2925	215
Low to medium	31	926	1279	1332	0
Medium	5	412	786	634	0
Medium to high	21	210	333	115	0
High	31	3	388	32	0
1998					
Low	2844	5369	2862	1840	358
Low to medium	2	977	1530	1191	0
Medium	0	190	867	464	0
Medium to high	0	140	513	138	0
High	0	6	328	35	0
1999					
Low	2162	5129	5350	3635	217
Low to medium	143	93	214	1142	0
Medium	0	0	0	71	0
Medium to high	30	0	0	1	0
High	27	0	0	0	0
2000					
Low	1595	5934	3096	1490	335
Low to medium	908	595	938	1265	0
Medium	502	30	681	766	0
Medium to high	131	0	173	180	0
High	57	0	0	1	0
2001					
Low	1869	4360	4454	3108	217
Low to medium	68	448	328	52	0
Medium	243	249	371	5	0
Medium to high	145	113	121	0	0
High	57	1	0	0	0

Variables include classes of WCR abundance (WCR class) and elevation classes, including Class 1 (494–499 m), Class 2 (500–504 m), Class 3 (505–509 m), Class 4 (510–514 m) and Class 5 (515–519 m).

Table 8 Contingency statistics for elevation and western corn rootworm (WCR) abundance

Year	Chi squared	d.f.	Cramer's V	*P*
1997	2160	16	0.17	<0.001
1998	4331	16	0.23	<0.001
1999	2453	16	0.18	<0.001
2000	3821	16	0.23	<0.001
2001	1156	16	0.13	<0.001

Variables include year, chi squared, degrees of freedom (d.f), Cramer's V coefficient and probability value (*P*).

spatial relationships. Even though only a few landscape metrics were computed in this study, a small set of landscape indices captured significant aspects of shifting patterns of vegetation and WCR abundance. In addition, we may have underestimated some of the relationships of landscape composition and WCR distribution because mortality from insecticide application was not accounted for. Further research at other areawide sites varying in landscape structure, soil textures and elevation may be useful to determine the significance of these variables on WCR metapopulation dynamics across the US Corn Belt. Overall, our research emphasizes the potential role for GIS to provide information on interactions between landscape structural characteristics, edaphic factors and insect pest population dynamics. The technique also can be extrapolated to larger areas and can include Landsat satellite images, climatic data layers and beneficial insect data layers. We can then use these data layers in GIS models to find patterns in the landscape that promote high insect population density patches and, consequently, to improve pest management strategies. Landscape planners, agricultural managers and producers can benefit from this research by understanding the complex interactions of WCR population dynamics and landscape variables.

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References

Abler, R., Adams, J.S. & Gould, P. (1971) *Spatial Organization: The Geographer's View of the World*. Prentice Hall, Englewood Cliffs, NJ.

Bonham-Carter, G.F. (1994) Raster and vector spatial data models. *Geographic Information Systems for Geoscientists: Modelling with GIS* (ed. by D. F. Merriam), 1st edn, pp. 51–82. Elsevier Science Inc., Tarrytown, NY.

Brewster, C.C., Allen, J.C. & Kopp, D.D. (1999) IPM from space: using satellite imagery to construct regional crop maps for studying crop–pest interaction. *American Entomologist*, **45**, 105–117.

Buckman, H.O. & Brady, N.C. (1969) Some important physical properties of mineral soils. *The Nature and Properties of Soils*, 7th edn, pp. 41–69. The Macmillan Co, New York, NY.

Chandler, L.D. & Faust, R.M. (1998) Overview of areawide management of insects. *Journal of Agricultural Entomology*, **15**, 319–325.

Chandler, L.D., Coppedge, J.R., Edwards, C.R., Tollefson, J.J. & Wilde, G.E. (2000) Corn rootworm area-wide management across the United States. *Area-Wide Control of Fruit Flies and Other Insect Pests* (ed. by K. H. Tan), pp. 159–167. Penerbit Universiti Sains Malaysia, Penang.

Chiang, H.C. (1973) Bionomics of the northern and western corn rootworms. *Annual Review of Entomology*, **18**, 47–72.

Chou, Y. (1997) *Exploring Spatial Analysis in GIS*, 1st edn. OnWord Press, Sante Fe, NM.

Coats, S.A., Tollefson, J.J. & Mutchmor, J.A. (1986) Study of migratory flight in the western corn rootworm (Coleoptera: Chrysomelidae). *Environmental Entomology*, **15**, 1–6.

Eastman, R.J. (2001) *Guide to GIS and Image Processing, 1. (Idrisi Computer Software) Idrisi Production*. Clark University, MA.

Forman, R.T.T. (1995) *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge University Press, New York, NY.

Forman, R.T.T. & Godron, M. (1986) *Landscape Ecology*. John Wiley & Sons, New York, NY.

Gray, M.E., Steffey, K.L. & Oloumi-Sadeghi, H. (1993) Participatory on-farm research in Illinois cornfields: an evaluation of established soil insecticide rates and prevalence of corn rootworm (Coleoptera: Chrysomelidae) injury. *Journal of Economic Entomology*, **86**, 1473–1482.

Hargis, C.D., Bissonette, J.A. & David, J.L. (1998) The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology*, **13**, 167–186.

Harrison, S. & Taylor, A.D. (1997) Empirical evidence for metapopulation dynamics. *Metapopulation Biology: Ecology, Genetics, and Evolution* (ed. by I. A. Hanski and M. E. Gilpin), pp. 27–42. Academic Press, San Diego, CA.

Hatakeyama, A., Mitchell, A., Booth, B., Payne, B., Eicher, C., Blades, E., Sims, I., Bailey, J., Brennan, P. & Stephens, S. (2000) Symbolizing your data. *Using Arcmap* (ed. by M. Minami), pp. 133–166. ESRI Press, Redlands, CA.

Hill, R.E. & Mayo, Z.B. (1980) Distribution and abundance of corn rootworm species as influenced by topography and crop rotation in eastern Nebraska. *Environmental Entomology*, **9**, 122–127.

Johnston, C.A. (1998) GIS data. *Geographic Information Systems in Ecology* (ed. by J. H. Lawton and G. E. Likens), pp. 18–48. Blackwell Science Ltd, Malden, MA.

Kantack, B.H., Walgenbach, D. & Berndt, W.L. (1970) *Corn Rootworm Control in South Dakota*. South Dakota Extension Service, Brookings, South Dakota.

Kaul, R.B. (1986) Physical and floristic characteristics of the Great Plains. *Flora of the Great Plains* (ed. by Great Plains Flora Association), pp. 7–10. University Press of Kansas, Lawrence, KS.

Kirk, V.M., Calkins, C.O. & Post, F.J. (1968) Oviposition preferences of western corn rootworms for various soil surface conditions. *Journal of Economic Entomology*, **61**, 1322–1324.

Kopp, S., Borup, B., Willison, J. & Payne, B. (2002) Performing spatial analysis. *Using Arcgis Spatial Analyst* (ed. by J. McCoy & K. Johnston), pp. 119–187. ESRI Press, Redlands, CA.

Krajewski, S.A. & Gibbs, B.L. (2001) *Gridding Algorithms. Understanding Contouring*, pp. 19–41. Gibbs Associates, Boulder, CO.

Landis, D.A. (1994) Arthropod sampling in agricultural landscapes: ecological considerations. *Handbook of Sampling Methods for Arthropods in Agriculture* (ed. by L. P. Pedigo and G. D. Buntin), pp. 16–31. CRC Press, Boca Raton, FL.

Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, **45**, 175–201.

Levine, E., Spencer, J.L., Isard, S.A., Onstad, D.W. & Gray, M.E. (2002) Adaptation of the western corn rootworm to crop rotation: evolution of a new strain in response to a management practice. *American Entomologist*, **48**, 94–107.

McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) *FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps*. University of Massachusetts, Amherst, MA (http:www.umass.edu/landeco/research/fragstats/fragstats.html).

Metcalf, R.L. (1986) *Methods for the Study of Pest Diabrotica* (ed. by J. L. Krysan and T. A. Miller), pp. vii–xv. Springer-Verlag, New York, NY.

Monmonier, M.S. (1977) *Maps, Distortion, and Meaning (Resource Paper No 75–4)*. Association of American Geographers, Washington, D.C.

Onstad, D.W., Joselyn, M.G., Isard, S.A., Levine, E., Spencer, J.L., Bledsoe, L.W., Edwards, C.R., Di Fonzo, C.D. & Wilson, H. (1999) Modeling the spread of western corn rootworm (Coleoptera: Chrysomelidae) populations adapting to soybean-corn rotation. *Environmental Entomology*, **28**, 188–194.

Ott, L., Larson, R.F. & Mendenhall, W. (1983) *Statistics: A Tool for the Social Sciences*. Duxbury Press, Boston, MA.

Pulliam, H.R. & Danielson, B.J. (1991) Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist*, **137**, 50–66.

Roberts, E.A., Ravlin, F.W. & Fleischer, S.J. (1993) Spatial data representation for integrated pest management programs. *American Entomologist*, **39**, 92–107.

Ruesink, W.G. (1986) Egg sampling techniques. *Methods for the Study of Pest Diabrotica* (ed. by J. L. Krysan and T. A. Miller), pp. 83–99. Springer-Verlag, New York, NY.

SAS Institute, Inc. (1998) *Statview: Statview Reference*, 2nd edn. SAS Institute Inc., Chicago, IL.

Siegel, S. & Castellan, N.J. Jr (1988) *Nonparametric Statistics for the Behavioral Sciences*, 2nd edn. McGraw-Hill Inc., New York, NY.

Siegfried, B.D., Meinke, L.J. & Scharf, M.E. (1998) Resistance management concerns for areawide management programs. *Journal of Agricultural Entomology*, **15**, 359–369.

Smith, A.T. & Gilpin, M. (1997) Spatially correlated dynamics in a pika metapopulation. *Metapopulation Biology: Ecology, Genetics, and Evolution* (ed. by I. A. Hanski and M. E. Gilpin), pp. 407–428. Academic Press, San Diego, CA.

Stow, D.A. (1993) The role of geographic information systems for landscape ecological studies. *Landscape Ecology and GIS* (ed. by R. Haines-Young, D. R. Green and S. H. Cousins), pp. 11–21. Taylor & Francis Inc., Philadelphia, PA.

Thomas, C.D. & Hanski, I.A. (1997) Butterfly metapopulations. *Metapopulation Biology: Ecology, Genetics, and Evolution* (ed. by I. A. Hanski and M. E. Gilpin), pp. 359–386. Academic Press, San Diego, CA.

Tollefson, J.J. (1986) Field sampling of adult populations. *Methods for the Study of Pest Diabrotica* (ed. by J. L. Krysan and T. A. Miller), pp. 123–146. Springer-Verlag, New York, NY.

Tollefson, J.J. (1998) Rootworm areawide management program in Iowa. *Journal of Agricultural Entomology*, **15**, 351–357.

Tollefson, J.J. & Calvin, D.D. (1994) Sampling arthropod pests in field corn. *Handbook of Sampling Methods for Arthropods in Agriculture* (ed. by L. P. Pedigo and G. D. Buntin), pp. 434–473. CRC Press, Boca Raton, FL.

Turner, M.G. (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecological Systems*, **20**, 171–197.

Turpin, F.T. & Peters, D.C. (1971) Survival of southern and western corn rootworm larvae in relation to soil texture. *Journal of Economic Entomology*, **64**, 1448–1451.

Wiens, J.A. (1997) Metapopulation dynamics and landscape ecology. *Metapopulation Biology: Ecology, Genetics, and Evolution* (ed. by I. A. Hanski and M. E. Gilpin), pp. 43–62. Academic Press, San Diego, CA.

Wilde, G.E., Whitworth, R.J., Shufran, R.A., Zhu, K.Y., Sloderbeck, P.E., Higgins, R.A. & Buschman, L.L. (1998) Rootworm areawide management project in Kansas. *Journal of Agricultural Entomology*, **15**, 335–349.

Zar, J.H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice Hall Inc., Englewood Cliffs, NJ.

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